

UNCLASSIFIED

AD NUMBER
AD833284
NEW LIMITATION CHANGE
TO Approved for public release, distribution unlimited
FROM Distribution authorized to U.S. Gov't. agencies and their contractors; Critical Technology; AUG 1966. Other requests shall be referred to Department of the Army, Fort Detrick, Attn: Technical Releases Branch, Frederick, MD 21701.
AUTHORITY
Fort Detrick/SMUFD ltr dtd 15 Feb 1972

THIS PAGE IS UNCLASSIFIED

AD833284

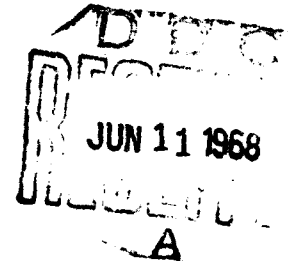
TRANSLATION NO. 1789

~~REFERENCE~~ CA-18-064-D6-0030(A)

DATE: 4 August 1966

DDC AVAILABILITY NOTICE

Reproduction of this publication in whole or in part is prohibited. However, DDC is authorized to reproduce the publication for United States Government purposes.



STATEMENT #2 UNCLASSIFIED

This document is subject to export controls and each transmittal to foreign governments or foreign nationals may be made only with prior approval of _____

DEPARTMENT OF THE ARMY

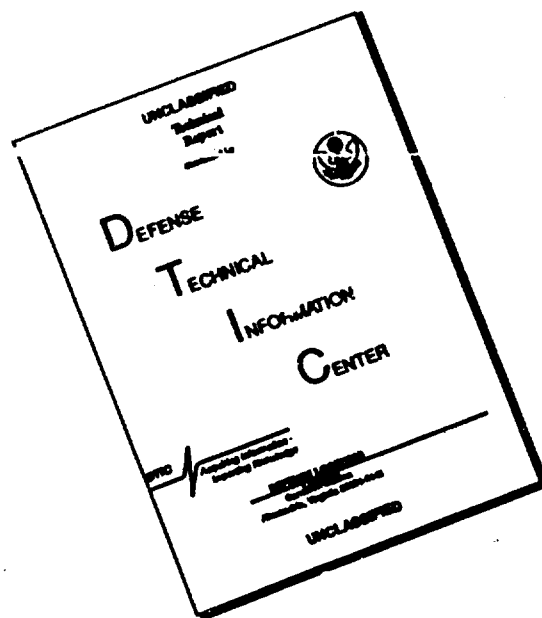
Fort Detrick

Frederick, Maryland

21701

18

DISCLAIMER NOTICE



**THIS DOCUMENT IS BEST
QUALITY AVAILABLE. THE COPY
FURNISHED TO DTIC CONTAINED
A SIGNIFICANT NUMBER OF
PAGES WHICH DO NOT
REPRODUCE LEGIBLY.**

1789

CA-18-064-D6-00030(a)

T-433-1

4 August 1966

HIGH PARASITES, OROBANCHACEAE

Schnucker, W.

This translation is protected by international copyright law and is provided solely for internal use at these laboratories. Reproduction or release by recipients is prohibited. Queries concerning availability should be directed to the Technical Releases Branch, Technical Information Division.

FOR DESK USE ONLY. Not for use in Dept of Army Publication. See AR 310-1, Par. 16.

Orobanchaceae

This family undoubtedly is tied in with the Scrophulariaceae with their varied semi-parasites in a fashion which of course is not exactly known; this family contains only the holosaprophytic species. The by far most important and best known genus here is represented by the Orobanche. Livera combined 7 genres of the families into a separate family called the Aeginetiaceae (Figure 49); this separate family should be placed between the Scrophulariaceae and Orobanchaceae.

Orobanche (cf., Beck-Mannagetta (1 and 2)) includes about 100 species, almost all of them from moderate-climate Europe and Asia, 1 each from Chile, North America, and Western Australia, 1 from the Cape Country, (introduced?). All are root parasites with hypocotyledon nodules ~~tubers~~ (Figure 50) and with highly-developed layer shoots. The home of these plants is frequently located in dry areas (prairies and similar areas). (Figure 51).

Parasitism has reached a high stage in the Orobanche and among the other genres. Of course there are species which can grow on a rather wide variety of host plants; but others are extensively specialized. (*Cistanche tubulosa* is found on such widely different hosts such as *Calotropis* (Asclep.) and *Acacia* (leg); according to Tiagi.) *O. crenata* is reported to parasitize only on the secondary roots of Leguminosae. Of the 24 Orobanche species in central Europe, for instance, 4 are not at all choosy but they nevertheless very clearly favor certain individual affinity circles; 3 are essentially confined to a single big family, 7 are confined to a rather narrow circle of affinity or relationship, and 10 are confined to 1 or just a few related species. No less than 10 are found only or predominantly on Composites (5 of them almost only on *Artemisia*), 4 are found mostly on Leguminosae. Monocotyledons, Gymnosperms and Pteridophytes apparently are never hit. But if we also add some of the rather unusual hosts, then we get 60 and more host species in some of the Orobanche. Similarly, many of them can be raised also on all kinds of garden vegetables. On the other hand, we also know of certain biological races. Parievskaja found strong immunity differences among hemp races against *O. ramosa*. As far as *O. cumana* is concerned, we have various aggressive races, on the one hand (in the Don and in the Kuban region); on the other hand, some of the *Helianthus* species are completely immune also against the aggressive Orobanche races whereas others are only relatively immune (Shdanow, 1-3). The seeds (Figure 52) are very small; they contain oil and they are also very numerous (1 plant may produce more than 100 thousand seeds in several dozen capsules). According to Kadry and Tewfic, a blooming sprout produces 4 mg of seeds; this would be about 40,000 seeds (1 seed = 10^{-4} mg). This seed weight roughly corresponds to that of the lightest orchid seeds. The seeds retain their germinating power for a long time (according to Kadry and Tewfic, *O. crenata* retains its germinating power for 10 years); because they are so small they can easily be washed into the soil. On the other hand, because of their loose, rather odd rough surface, they are suited for dissemination by means of the wind. In a fat-rich endosperm we have the embryo which contains very few cells and which is hardly subdivided or organized (no cotyledons); this embryo consists only of the epidermis and 1 or just a few rows of cells (Figure 52).

Germination occurs only in the presence of a host root. This somewhat challenged finding has recently been confirmed repeatedly (Pearsall, and others). Kadry and Tewfic found that this stimulus extends at most for a distance of 3 cm and issues only from plants that are capable of blooming. Barcinski found that roughly half of the seeds germinate when the expressed juice of the host is added; this, in other words, involves all of the seeds that are in any way capable of germinating; without this host juice there is almost no germination. The stimulating substance cannot be highly specific; Chabrolin found this effect also with expressed root juices which did not come from the host roots; Brown and associates obtained an effective substance from *Linum* which is not considered as a host plant here. The effective substance [active substance, vitamin], according to these authors, would appear to contain neither nitrogen nor one of the well known carbohydrates. This might possibly involve Vitamin B and Auxin. Germinal stimulation has also been used in practice (sprinkling of seed beds with *Helianthus* extract prior to planting). According to Stanganeli the rather low degree of inclination toward germination might be based on the nature of the membrane of the seed shell (lignin, tanning substances). According to Kadry and Tewfic, the seed shells are liquified and cutinized.

During germination (Figure 52) the germ is extended into a thread-like structure (with a length of up to about 1 mm). After it reaches a host root, the hypocotyledon is turned into a little nodule (Figure 52). The root pole, which does not have a root cap, gets a hold on the root surface with the help of papilla cells and, simply dissolving the tissue in front of it, penetrates into the root, until it establishes contact with the vascular tracks (Figure 53). There can also be outgrowths to the side. The entire shape should be construed as a transformed, ramified root system (Troll); Kadry and Tewfic however challenge this view. The sprout hole remains stuck in the endosperm during germination and usually dies off; the sprout piece which corresponds to the hypocotyledon swells up into a knob which sits on top of the host root. Along this knob we have the blossom stands developing endogenously with the scale leaves; these blossom stands [inflorescences] develop in the form of subcotyledonary adventive sprouts (Rauh). At the base of the tuber or knob we mostly find developing short, thick adventive roots (without a clearly developed root cap) which in some species however can become quite long and which can produce both secondary haustoria and blooming root sprouts (for a detailed description of this development, see Koch, 2) (cf., also Figure 58).

In many cases, the bark tissue portions of the host form around the point of penetration and constitute a kind of meristema which produces a hump on which the tuber or knob is then developed; the outgrowths of the haustorium now grow into this hump. X-ray fluorescence caused Borsi to think -- rather incorrectly -- that the connection (with the *Faba* roots) is quite superficial. In some species (*O. minor hederæ*, etc.) numerous, long-drawn-out outgrowths develop out of the primary sector, moving through the bark tissue [cortical tissue] of the host; along these outgrowths we can find blossom sprouts, especially after the primary haustorium has died off. We might call this vegetative multiplication or we might say that the parasite has as a result become lasting. In the haustorium, the conduit tracks are mostly differentiated with the frequently quite primitive water tracks. As a result of

the cell division, both in the parasite tissue and in the host tissue, the tissues of the former are so completely combined with the tissue of the latter that the parasite in the end appears almost as if it were a part of the host or that it sits on it like a perhaps on-grown graft-scion. All of this is very easy to put down on paper but it is just about impossible to understand the causal mechanism today. The host root piece very often dies off above the point of attack; then it looks on the outside as if *Orobanche* were an independent plant with its own root. It lives for some time now partly at the expense of the stored reserve substances. In many species, marginal cells of the haustorium in the end grow into haustorial tubes. This occurs (Schumacher and Halbsguth) especially in connection with the attack upon the sieve tubes. The haustorial cells force their way in between these tubes and compress them from the top, without any Callus developing between them (Figure 54). Here no sieve-plate-like connections are formed. The sieve tubes are grasped vise-like by the haustoria especially in the region of the sieve plates. The haustoria may also be divided longitudinally and they may gradually grow forward in the sieve portion. Oddly enough the otherwise so sensitive sieve tubes are preserved longest and, in connection with the haustorial cells, are sometimes found in the midst of completely destroyed host tissue. But sieve tubes are not differentiated in the parasite tissue (according to findings on *O. ramosa*); we can only recognize plasma-rich rows of cells. Between the parenchyma cells of the host, respectively, the parasites, it was possible to prove the presence of corresponding spots or specks, respectively, plasmodesma; but this could not be done in the connecting surfaces with the sieve tubes. By the way, K. O. Miller did not succeed in successfully grafting quite young blossom sprouts of the *Orobanche* species onto their host plants.

Because of the ease of penetration, the development activity of the host tissue in favor of the parasites, the connection with the sieve tubes, and so on, we can prove the advanced stage of development of parasitism in *Orobanche*.

Chlorophyll is found in *Orobanche* at most in a very small quantity. Stomata are found in small numbers on the stalks, leaves, and blossom parts (*Solereder*); in some gemuses (*Phelipaea*) they are absent.

The blossoms of the *Orobanche* species (Figures 55-57), which are annual or perennial, are zygomorphous, homogamous, or protogynous insect blossoms with nectaries at the bottom of the blossom (these nectaries are missing in some species) and we also have various odors here. These plants, depending upon the species, are visited by bees, wasps, etc. In some species the entire development is very fast and this is absolutely necessary in the case of parasites on annual hosts. *Orobanche major* however took at least 4 years until blossom time in a planting experiment conducted by Nilsson on *Centaurea Scabiosa*. In the case of *O. uniflora* we have forms with diploid parthenogenesis (Jensen). In *Cistanche* the Archespore mother cell directly grows into a megaspore mother cell (Kadry).

The chemical composition (of *O. gracilis*) is as follows: Water 76, dry substance 24. Ash 2.9% of dry substance (47 K_2O ; 0.2 Na_2O ; 8.5 CaO ;

9.2 P_2O_5) (Wehmer). The findings of Nicoloff are quite interesting (the numbers in the parentheses give the figure for the host root attacked): N 1.6 (2.2)% of the dry substance; ash 9 (16)% of dry substance. In ash 37 (18)% K_2O ; 1.5¹ (20)% CaO ; 2 (5)% MgO ; 6.5 (2.2)% P_2O_5 . The differences between the host and the parasite thus are quite considerable and are quite similar as in the case of *Cuscuta*. According to Haller, the dry substance of *O. ramosa* is quite uncommonly rich in pectin-like substances; the cell walls almost look as if they consist of pectocellulose.

There are a number of reference points here for the details of metabolism. Zakharov in the case of *O. cumana* on *Helianthus* found an increase in the form of attack in the short-day plant; of course, this can be interpreted in various ways. *Orobanche* can also blossom (on *Coleus*) if the host does not reach the blossoming phase; the host, for its part, does not stimulate the blossoming phase. The parasite accordingly would appear to be blossom-hormonotrophic, although perhaps the host blossoming substance might promote the blossoming of the parasite (Kribben). Holdsworth and Nutman on the other hand in the case of *Orobanche minor* on red clover found that the blossoming phase completely depends upon the blossoming phase of the host. Narasimhan and Thirumalachar in Bihar, India, found *O. cernua* attacked massively by a kind of *Sclerotinia* rot; the host plant remained healthy but could not be infected artificially. Alekseev grafted vulnerable *Helianthus* races onto resistant roots; it was impossible to detect any influence upon the resistance of the plants that sprang from the seeds of the graft shoot.

According to Richter, *O. cumana* transpires, per unit of area or surface, roughly just as much as the host (*Helianthus*). The stomata apparatus is very heavily involuted and does not play a role here. According to Bereznegovskaja, vulnerable *Helianthus* races, after attack, reduce their transpiration whereas highly resistant races increase it. Only in the former is the dry weight and the development of the roots reduced in any way whereas in the latter it is even increased. A suction force difference of about 5 atm between the host and parasite was established by Bergdolt.

Orobanche damages only through the withdrawal of substance. In some cases it can have a devastating effect upon some crop plants through mass development (*O. ramosa* on tobacco; *O. minor* on clover; *O. cumana* on *Helianthus*; according to Blanchard, *O. speciosa* on peas in Algiers). By adding a Hg-containing organo-silicate, it was possible to prevent the germination of the parasite without damaging the host (Blanchard). *O. cumana*, of which we have various virulent physiological races, can extraordinarily reduce the yield and oil content of *Helianthus* (Shdanow, 1); *Orobanches* are sometimes parasites that are very dangerous on red clover (Werneck).

In the case of *Aeginetia*, the embryo, according to Kusano, is particularly small and undifferentiated. During germination, which can take place only in the presence of a host root, the epidermis cells grow out very heavily along the root pole; one of them develops into a long, septed hair which can also become ramified, which grasps the root of the host like a climbing plant and

which then pulls the embryo toward it. *Aeginetia* lives as a parasite only on monocotyledons; the germination stimulus however can also issue from dicotyledons and even from Pteridophytes. Hedayatullah and Saha found *A. pedunculata* especially on sugar cane with whose roots the parasite organs form a dense, confused mass.

GENERAL PART; SUMMARY

The holoparasitic blossoming plants, because of their odd shape and development, attracted the attention of researchers rather early but were often interpreted in a mistaken fashion. As early as 1841 Junghuhn, the very successful explorer of Java, thought that the roots of certain tropical trees directly bring out the *Balanophora* blossoms as a result of "a certain change in the juices" -- "under certain circumstances." But he was not quite happy with this idea. Even before that, in 1818, Dr. J. Arnold, the man who accompanied Sir Th. St. Raffles, discovered the giant blossoms of *Rafflesia* in Sumatra. The foundation of our knowledge on the phanerogamous parasites was developed primarily by Fr. Unger (1840), G. A. Chatin (since 1858) and H. Graf Zu Solms-Laubach (since 1868). Many facts were unknown for a long time or at least we were not sure of them; this is of course not surprising considering the partly so rare and so difficult to preserve plants, plants which in many cases are hardly cultivable. *Orobanche* species are easy to cultivate (cf., Nilsson), and the same goes for *Aeginetia* and *Cuscuta*. Today the morphology has been explored at least in its rough outline; the physiology, on the other hand, has been explored to a much lesser extent -- last but not least because of the experimental difficulties. In recent times -- when many botanists were hardly interested in plants other than those laboratory plants which are suited for thorough basic research -- very little attention has been devoted to those forms which more or less are considered "oddities."

There has hardly been one case in which holoparasitism of certain blossoming plants, in other words, a property which in the final analysis is physiological, has been established directly, although this has been done on the basis of rather compelling evidence. The shortage of chlorophyll would preclude the normal autotrophic form of nutrition; the morphological combination with the host plant makes it obvious to assume that the latter provides nutrition through assimilates. Since there is obviously no other possibility, this assumption is bound to be correct.

Some of the *Orobanchaceae* and the genus *Cuscuta* have a very small chlorophyll content which varies according to the species and the circumstances; this is a remnant of the greater chlorophyll content of the normal, grain ancestors. In some of the "hemiparasitic" although still grain *Scrophulariaceae* the chlorophyll content is relatively small; this would lead us to think that a host might also supply assimilates here. With the exception of *Cassytha*, the chlorophyll content in none of the holoparasites is even remotely great enough to enable their own CO₂ assimilation to play a major trophic role. The rather odd fact of the extensive coupling of chlorophyll content and the possession of stomata generally is expressed also in the holoparasites (cf., Linsbauer and Ziegenspeck), but this is not always the

case. Only *Cassytha* has abundant Stomata; comparatively many Stomata are also found in *Lathraea*, even along the underground parts, and quite a few are found in *Cynomorium*. Oddly enough, the *Lennoaceae* also have relatively many Stomata. In all of the others, these Stomata (also on the scale leaves) are present at most in a very small number or are entirely missing; this is apparently true in the case of the *Balanophoraceae*, some of the *Rafflesia* species (for instance *R. patma*) and some of the *Orobanchaceae* (for instance *Phelipaea*). On the other hand, Stomata are found on the scaly leaves of some of the *Rafflesiaceae* (for instance, *Mitrostemon*, *Rhizanthus*, *Cytinus*, *Pilostyles*), in other words, in forms with otherwise extreme involution of the vegetative *Cormus*. Very often, however, they are heavily involuted and they are more or less without function. There is not a single whole parasitic species with well-developed and simultaneously chlorophyll-free foliage leaves. It will be difficult to determine whether the phylogenetic development occurred via the involution of chlorophyll and subsequent leaf reduction or *visa versa*. Perhaps the various series behaved in a different fashion in this respect. At any rate, the extensive coupling of 2, in themselves independent involution phenomena, is quite interesting to note here. We must assume that there is a development-physiology causal connection, unless we want to risk engaging in some of the more mystic thoughts.

The vegetative sprout system is rather normally developed only in the winding forms (*Cuscuta* and *Cassytha*) and to some extent also in *Lathraea* and among the *Lennoaceae*. The extramatrix branches of the *Hydnoraceae* are "in between shapes or forms" -- that is to say, between the sprout and the root. In all of the others the main axis, etc., is represented by hypocotyledon and root sprouts which very often are inflorescences provided they do not spring from intramatrix "strands" made of floral pillows and similar organs of an uncertain morphological nature. A reasonably developed root system can be found in *Cassytha* species, *Lennoaceae*, where the root character of the haustoria however is not quite certain, as well as *Lathraea* and perhaps also the few holoparasitic *Santalaceae*. But here again the roots -- which in most cases are more abundantly ramified -- soon try to establish contact with the host roots. The intramatrix parts of all of the other groups -- those extremely odd systems of strands, hyphens, haustoria, etc., which differ so greatly from the norm -- in most cases can be interpreted as heavily modified root systems. They are extremely well adapted to their special function and, as far as their shape goes, they are mostly more or less involuted, up to the "giant haustorium," which has been used in referring to the entire vegetative system of the *Rafflesiaceae*. As far as we know, in all of these forms, it is already the germ root, which often hardly reveals any of the characteristics of a root and which is turned into the haustorium which penetrated into the host, just like the sprout-born adventive haustoria of *Cuscuta* and *Cassytha*.

Regardless of the morphological interpretation -- which is altogether limited in highly derived forms -- we can compare the intramatrix system with a root system which keeps the plant family in the substrate and which takes on nutrient substances, in this case of course this would also include the organic substances. The penetration into the body of the host mostly takes place not through rough destruction and exploitation of host tissue,

but rather as part of a sliding or gradual growth between the cells, respectively, the tissues of the host, in such a manner that, in the end, the parasite looks almost like a part of the host plant also from the histological viewpoint. In addition to the ramification of the advancing strands, etc., we have, to a greater or lesser extent, also the distribution of the tips, etc., into long, thin threads, which then proliferate through the host tissue; Finally we also have single-row "Hyphens." In most of these cases, these "haustoria" do not penetrate into the cells themselves. But they are most likely in all cases the channels of the host; adequate translocation could otherwise not be achieved, especially in the often rather strikingly thin host roots. The details of the connections have been explored in some forms (*Cuscuta*, *Orobancha*, *Rafflesia*). The completeness of the connection is not infrequently achieved through corresponding tissue formation activity in the host tissue under attack; this can be seen most impressively in the case of the *Balanophoraceae* whose partly gigantic tubers represent almost specifically constructed complexes made of newly formed host tissue and parasite tissue. Some people have been quite justified in pointing to the gal formations and their "alien purposes." Rough or coarse malformations on the host (lignified swellings, witch's brooms, etc.) are generally not caused here. The holoparasitic blossoming plants are on the dividing line between viruses and mere tests (Gutmann).

The anatomical differentiation is very little almost always, even in the case of the thicker, intramatrical strands, etc. We may find bundles of vessels, mostly heavily reduced. Normally developed channel strands often are formed only if those inflorescences are started where well-differentiated channel or vessel bundles are the rule. In a very interesting study, Cutter proved that, in the case of holoparasites (similar to the case of the holosaprophytes), the "apical organization" of the vegetation points of the sprout axes, providing there are any of these axes that can be identified, is not abnormal (he showed this for *Cassytha*, *Cuscuta*, *Balanophora* and *Lathraea*; he also showed it for *Phoradendron* and *Loranthus*). He reported that in these parasitic (and saprophytic) forms phloem is the "preponderant vascular tissue."

According to morphological findings it is quite clear that the parasite gets all of the substances it needs through the host. For water and mineral substances, the situation is rather simple; suction force differences have been established in some cases (*Cuscuta*, *Orobancha*, *Lathraea*) (cf., also Senn). Nevertheless, the mechanics of the flow of these substances into the parasite, especially into the inflorescences, still creates all kinds of problems; the obviously very intensive metabolism and substance consumption in the rapidly developing, often very massive inflorescences, will have to be studied in particular detail here. Very little seems to be known about the details of the organic substances. Does this involve only (or essentially) the absorption of carbohydrates (sugar) with which the parasite then continues to manage as if it had acquired them, itself, through the assimilation of CO_2 ? Or are albumin substances, etc., so to speak, digested, in other words, are they taken over, decomposed, and newly built up? Or Pora, Pop, Roska and Radu thought that there was a closer relationship here also with respect to the organic substances

in the green semi-parasite (*Viscum album*) on the basis of the finding that the pharmacological effect of extracts from mistletoe which had grown on various species of trees, varies in intensity -- more specifically, parallel to the intensity or effectiveness of host cortex extracts. With the help of isotopes we might be able to learn some more about these conditions which we know very little about today. Cutler thinks that he can assume -- on the basis of morphological reasons (abundant presence of starch and mechanical tissues) -- that the carbohydrate supply is mostly quite adequate and that the nitrogen supply probably constitutes the limiting factor. It is certain that the parasite can also absorb specific substances (viruses, blossom-forming substances) (*Cuscuta*, *Orobanchae*). In a mineral nutrient solution, to which only cane sugar was added, it has in the meantime been possible to get *Cuscuta* to develop full blooms.

The holoparasitic blossom plants of course often are propagated vegetatively in the form of rhizoma with shrubs (root sprouts), although this essentially happens through the seeds. On the whole, their blossoms are much more conservative than the highly transformed vegetative parts. The inflorescences axes, with their leaf scales, their bundles of vessels, and so on, differ far less from the norm than the purely vegetative parts. As for the rest, the blossoms reveal a tremendous variety, from the rather complicated structure of the giant blossoms of *Rafflesia* (with a diameter of almost 1 meter) all the way to the highly simplified dwarf blossoms (female blossoms of *Balanophora*). Most but not all groups share the "endeavor" to produce a large number of seeds although these might be very small and poor in nutrient substances. In one extreme, a few giant blossoms produce a tremendous number of macro- and microspores (cf., labyrinth formation in the giant ovaries of *Rafflesia*, formation of septa in the ovary of *Rafflesiaceae* and *Hydnoraceae*; labyrinths in the pollen sacks of *Rafflesia*, large number of anthers, respectively, pollen sacks in many *Hydnoraceae* but also in *Balanophoraceae*, etc.). In the other extreme we also have simple small blossoms being formed in tremendous numbers (*Balanophoraceae* but also *Cuscuta* and *Lentaceae*). This contrast can be found already in relatively closely related forms (*Rafflesia* -- *Pilostyles*). Involutions of a special kind do occur but are by no means the rule (naked, depressed seeds in *Prosopanche*, female blossoms of *Balanophora*). According to Bernard, it is interesting to note in a number of holoparasites (*Lathraea*, *Cytinus*, *Orobanchae*, *Phelipaea*), the strong reduction of the antipodes and the absence of the channel bundle in the funiculus. Completely normal, dorsiventral insect blossoms of medium size can be found in *Lathraea* and *Orobanchaceae*. The gametophyte development is almost always normal although we do find apogamy in some species (*Balanophora* species, *Hydnoraceae*?, *Cytinus*?). In general, pollination is thus necessary.

The pollination agents here usually are insects which are very little specialized from the blossom-biology viewpoint (flies, barbs, etc.). The otherwise mostly quite standardized blossoms of *Cuscuta*, *Lathraea*, and the *Orobanchaceae* are visited by bees, wasps, and bumble bees and others; they contain an abundant volume of nectare. In the tropic root parasites the

latter situation likewise develops but it does appear to be rather rare. The decoy or bait here would appear to be the color (sometimes entire, massive blossom stands are vividly colored, for instance, in Balanophoraceae) as well as odor substances of various kind, as usual. The blossoms of *Rafflesia* are "carrion insect blossoms," while those of *Hydnoraceae* perhaps likewise and in addition reveal some rather peculiar kettle-shaped insect traps.

Most of the other holoparasites -- like the *Rafflesiaceae* and the *Balanophoraceae* (see above) -- proceed according to the principle of producing a tremendous volume of small seeds. This is tied in with the difficulties encountered in successful germination for holoparasites. The seeds are relatively large only in *Cassytha*, *Cuscuta*, and partly in *Lathraea* (about 1 mg); in all of the others the seeds are much smaller and some of them are as small as grains of dust. But they almost always contain endosperm -- although in a very small quantity. The embryo is normally developed only in *Cassytha* and *Lathraea*; in *Cuscuta* it is somewhat normal (thread-shaped, without calyptra, cotyledons at most are only indicated vaguely); in all of the others it is unorganized, roundish, and often consists only of very few cells. This may be tied in somewhat to the seeds but it is certainly also tied in with the involution tendencies in the entire vegetative structure -- tendencies which are quite clearly developed already in the embryo. It is particularly interesting that both of these factors -- extreme smallness of seeds and low degree of organizational development of embryo -- can also be found in the likewise leafless and chlorophyll-less holosaprophytic blossom plants. In this case, successful germination requires assistance from the mycorrhiza fungus; in some of the other holoparasites (*Orobanchaceae*) there is a chemical stimulus which issues from the host root but in all cases the root must be present or must be within reach. However we know very little in this connection as far as the tropic holoparasites are concerned. *Cynomorium* at any rate does not appear to require any stimulation for its germination (Weddell), nor does *Cuscuta*. In the case of the fruits of the tropic root parasites which are found near the ground, the seeds are spread around whenever animals step on them or through the action of water, and so on; in the case of *Balanophoraceae*, *Orobanche*, etc., this might also be accomplished by the wind.

Holoparasitic blossoming plants are found both in the tropical and in the subtropical as well as in the temperate zone, both in the always humid and in the dry regions. Those, largely very adventurous forms from the families of the *Rafflesiaceae*, *Hydnoraceae*, and *Balanophoraceae* (almost 200 species) of course almost exclusively are found in the tropics whereas the groups from the tubiflora group are abundantly represented in the temperate zone, such as for instance the rather species-rich genera of *Cuscuta* and *Orobanche*, which, together, total 200 species. At some of the higher latitudes there are just a few species. In the north we found *Cuscuta epilinum* in Sweden up to 64°, *C. epithymus* up to 63°, and we can also find it in Greenland. *Lathraea* is found in Norway up to 61°. In the south, *Pilosyles pectinata* extends down to the strait of Magellan (51°). *Tozzia* is found in the Alps at an elevation of 2,400 m. *Juelia* was discovered in the Andes of Bolivia at an elevation of 3,850 m. Among the holoparasites we do not have any monocotyls (quite in

contrast to the holosaprophytes); all of them are herbs in the broader sense. Host specialization -- as far as we know today -- is sometimes quite broad (apparently even among the Balanophoraceae where one might expect the exact opposite) and sometimes it is very narrow (for instance in *Cytinus*, *Orobanche*). Medium degrees are quite frequent, that is to say, we have specialization to certain families or genera (for instance, *Mitrastemon*) or appearance on particularly suited main hosts and, simultaneously with this, on unrelated secondary hosts (for instance, *Cuscuta*, *Orobanche*). The holoparasitic blossoming plants damage their hosts more or less through the withdrawal of nutrient substances but they are hardly viruses, in other words, they are not pathogenic forms in the narrower sense of the word.

The phylogenetic derivation is quite clear in the case of the Orobanchaceae; the hemiparasitism, which is found in all gradations in the closely related forms, is stepped up here up to the extreme. The suitability of winding or climbing plants, such as *Cuscuta*, for using the supporting plant also trophically by forming haustoria, appears to be quite obvious to us in spite of all of the problems connected with this. The derivation of the Rafflesiaceae, Hydnoraceae, and Balanophoraceae from the related group of forms of the Santalales with its many hemiparasites appears to be quite obvious and can easily be performed on paper and may be quite correct in a number of points. But what in this case is merely convergence? We know very little about this. In this connection it is interesting to note that there are no stem or branch epiphytes in these families; otherwise it would be rather easy to figure out how a purely living epiphyte might become a parasite. It is obviously clear that the genesis of the holoparasites can be explained very easily from the viewpoint of Lamarck but that it can be explained with great difficulty from the viewpoint of Darwinistic selection.

FIGURE APPENDIX



Figure 49. *Aeginetia indica* on *Paspalum*.



Figure 50. *Orobanche speciosa*. Sprout base.



Figure 51. Orobanche spec. on abandoned pea field (sandy soil). Crete.

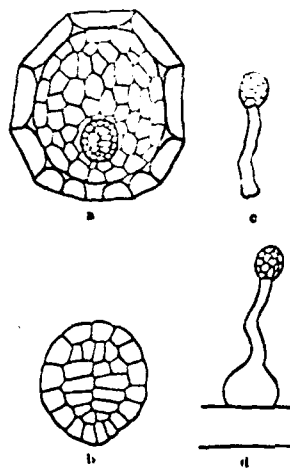


Figure 52 a-d. Orobanche. a--seeds; b--embryo; c--germination; d--youth stage with beginning tubur formation (diagram according to Kach).

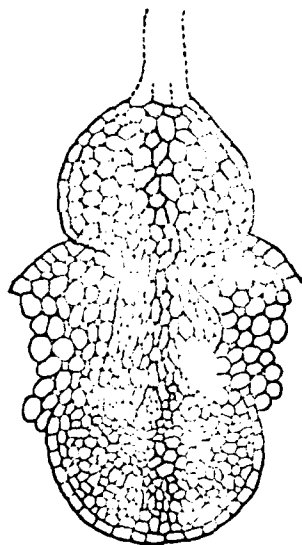


Figure 53. Orobanche. Haustorium in host tissue. Hypocotyl tubercle (as in Figure 52). Diagram.

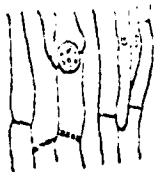


Figure 54. Orobanche. Connection to the sieve tubes. (Diagram according to Schumacher and Halbsguth.)



Figure 55. *Orobanche ramosa* on *Cannabis*.

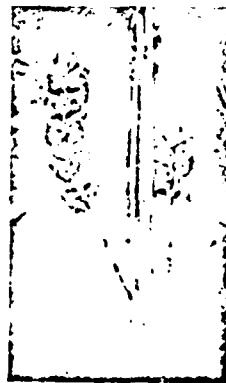


Figure 56. *Orobanche speciosa* on *Vicia Faba*.



Figure 57. *Orobanche uniflora* (from Engler-Prantl, 1897).

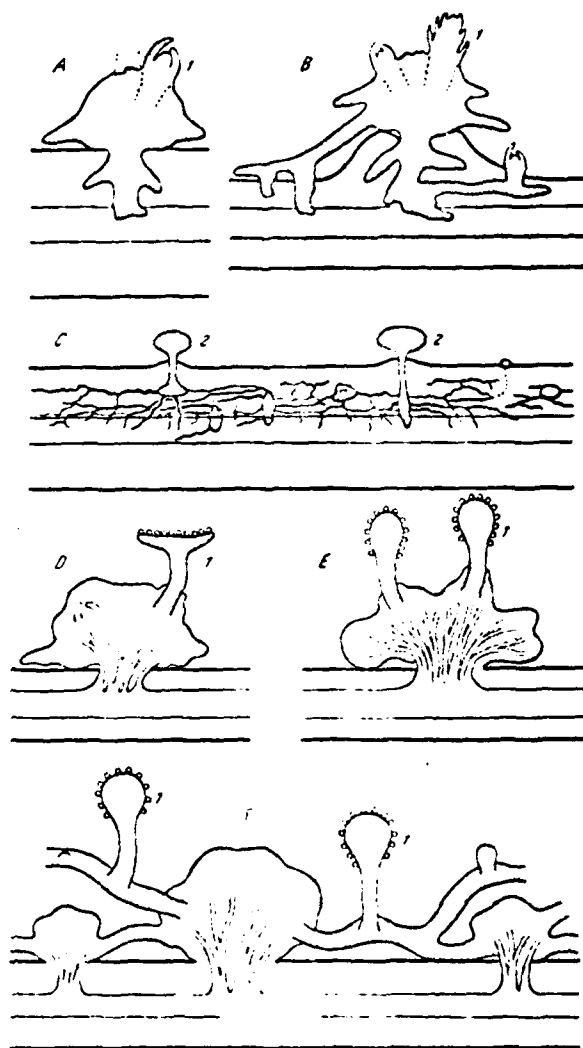


Figure 58 A-F. Diagram for the development of holoparasites and their connection with the hosts (1--blossom spans /inflorescences/; 2--individual blossoms). A and B--Orobanche; C--Rafflesia; D--Scybalium (Balanophoraceae); E--Balanophora; F--Helosis (Balanophoraceae).